

Factors Affecting Seedling Recruitment of *Allocasuarina distyla* and *A. nana* at Burnt and Unburnt Sites

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Allocasuarina distyla (Vent.) L. Johnson and *A. nana* (Sieb. ex Spreng.) L. Johnson are strongly serotinous shrubs, typically releasing their seed (as samaras) *en masse* after fire. In long-unburnt stands, however, there is a light seed rain from the canopy comprising some viable seed that will germinate after rain. This study examined several factors thought to be responsible for the notable absence of seedling recruits in unburnt vegetation. A sizable proportion of seeds falling from the canopy in dry weather is harvested by ants (seed half life approximately 3.5 days). Heating the soil surface had no effect on seedling establishment in either species. Emergence of both species was enhanced by increased experimental irrigation, suggesting that water deficits may be important in limiting establishment in the field. *A. distyla* established better in soil covered by litter, conceivably as a result of enhanced soil moisture levels. Recruitment of *A. nana* seedlings was reduced by litter on the soil surface, a result probably related to smaller seed size and failure to emerge from the litter. The enclosure of small mammals improved seedling recruitment at sites unburnt for 25 years, although increased number and sizes of recruits at experimental sites in burnt relative to unburnt vegetation are likely to have been mainly a result of both better light conditions and reduced competition.

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INTRODUCTION

It has long been observed that the seedling stage of the plant life cycle often exhibits the highest mortality (Miles, 1972; Harper and White, 1974; Harper, 1977). Thus patterns of plant distribution may be largely determined early in the life cycle by factors which affect seed germination and seedling survival. This paper presents the results of field and glasshouse experiments which focus on several such factors for *Allocasuarina distyla* (Vent.) L. Johnson and *A. nana* (Sieb. ex Spreng.) L. Johnson, two common and widespread plant species in the Sydney region.

A. distyla and *A. nana* are serotinous, holding their seed as samaras (henceforth referred to as seeds) for extended periods in woody 'cones' (infructescences) in their canopies. Seed is typically released *en masse* following the death of the branch on which it is held, usually as a result of fire (Pannell and Myerscough, 1993). However, a small amount of seed is also dispersed in a light seed rain from older cones on live branches and some of the seeds may be viable (Pannell and Myerscough, 1993). Despite this seed rain there is a notable absence of any seedlings in unburnt vegetation. Similar observations have also been made for other species in fire-prone environments (e.g. Christensen, 1971; Ashton, 1979; O'Dowd and Gill, 1984; Andersen and Ashton, 1985; Andersen, 1988; Keeley, 1992; Williams and Johnson, 1992).

The ways in which fire alters the biological and edaphic environment have been well documented (O'Dowd and Gill, 1984). For example: (1) fire removes much of the biolog-

ical opposition from a site so that there is more physical space for new growth (Evans, 1976); (2) considerable quantities of mineral and organic nutrients are added to the soil as ash (Pryor, 1963; Purdie, 1977) or as a result of direct heating of the soil (Humphreys and Craig, 1981; Bradstock, 1991); (3) the reduction in canopy cover allows more light into the understorey (McPherson and Muller, 1969; O'Dowd and Gill, 1984); (4) the removal of litter from the ground or the increase in litter cover due to scorched canopy litter fall can interact with evaporation from the soil (O'Dowd and Gill, 1984). Litter can interfere physically with establishing seedlings or alter the soil surface temperature as a result of changes in soil insolation levels (O'Dowd and Gill, 1984); (5) the burning of the canopy and of litter can halt the release of growth-inhibiting allelopathic toxins into the soil (del Moral and Muller, 1970); (6) a bushfire can interfere with the activities of granivores or herbivores (Leigh and Holgate, 1979). Several studies suggest that the *en masse* release of seed from serotinous plants after fire leads to a satiation of seed predators and an increased likelihood of survival for individual seeds (e.g. Ashton, 1979; Wellington and Noble, 1985; Andersen and Ashton, 1985; Andersen, 1988; Lamont *et al.*, 1991); (7) the various factors altered by fire can themselves interact with the time or season of burning. Bradstock and O'Connell (1988), for example, suggested that late summer/autumn fires favour establishment; (8) different species may respond to the effects of fire in contrasting ways if their requirements for germination and establishment differ (Bradstock and Myerscough, 1981; Bradstock, 1991).

In this study the influence of the following factors on the emergence and establishment of *Allocasuarina distyla* and *A. nana* seedlings was investigated: (1) the presence or absence of litter on the soil surface; (2) the effects of heat on the soil and the burning of litter; (3) the effect of germination and growth in soil from different provenances; (4) the effect of differences in soil moisture; (5) the effects of seedlings growing in stands at different times since fire; (6) stochastic effects attributable to random differences between sites; (7) the effect of seed harvesting by ants; (8) the effect of browsing by vertebrates. Factors 1, 2, 3 and 4 were investigated in a glasshouse experiment. Factors 5, 6, 7 and 8 were investigated in a second experiment under field conditions. Rates of seed harvesting by ants were further examined by observing the removal of seed from seed caches in unburnt vegetation. Rates of seed dispersal from the canopy were estimated by counting seed caught in traps beneath the canopy in a long unburnt coastal population of *A. distyla*.

METHODS

The seed rain

Seven circular seed traps were located randomly along a 30 m transect beneath the canopy within each of three dense populations of *A. distyla*, last burnt 25 years previously, on the Lambert Peninsula, Ku-ring-gai Chase National Park (NP). They were approximately 0.2m² in area and were made of finely woven nylon sewn onto a stiff wire frame. Their legs were coated thickly in sticky 'tanglefoot' to deter ants. The seed traps were visited at fortnightly intervals from May until August, 1990, and any captured seeds were collected and tested for germinability in the laboratory. At each site the density of cones and seed per area were estimated by counting the number of cones above a 1 metre-wide strip along the transect, multiplying by the average number of seeds per cone, and dividing by 30 to give an estimate in seeds/m².

Seed harvesting by ants

Four separate sites were chosen in tall heath stands on the Lambert Peninsula, Ku-ring-gai Chase NP, last burnt 25 years previously. The sites were all similar, being located on flat ground and dominated by *Allocasuarina distyla*. At each site eight closed petri dishes with three entry holes cut into their sides (approximately 1 cm²) were located ran-

domly along two independently laid 30 m transects. Ten *A. distyla* seeds were placed in four of the dishes, while ten of *A. nana* were placed in the other four. The transects at each site were laid randomly up to 50 m apart, running perpendicular to a baseline transect. The petri dishes were recovered after twenty-four hours and the number of seeds removed was recorded. The entire procedure was replicated four times, each time at independent (different) sites.

The results were analysed by a 4-factor ANOVA with species of seed treated as a fixed factor, time as a random factor, sites as a random factor nested in time and transects as a random factor nested in the times x sites interaction. During the course of the study petri dishes were found disturbed on a number of occasions, probably by birds or small mammals (Andersen and Ashton, 1985), so the data were analysed in two different ways: (1) using all the data, ignoring any possible effects of the disturbed petri dishes; (2) using an unbalanced data set with all values from disturbed petri dishes excluded from the analysis. In both analyses data were numbers of seeds removed in twenty-four hours from a depot of ten seeds. Variances were homogeneous, with degrees of freedom defined by the largest cell (Cochran's statistic = 0.0048, first analysis; = 0.032, second analysis; $k = 64$, $v = 3$; $P > 0.05$).

Glasshouse experiment

Soil and litter were sampled from three sites, one in Royal NP, one in Ku-ring-gai Chase NP and one in Bouddi NP in the Sydney region. At each site sixteen samples of soil and twenty-four of litter were chosen randomly from a 30 x 30 m grid. Soil was removed from an area of 15 x 15 cm² to a depth of approximately 10 cm and placed carefully into a one-litre plastic container with bottom drainage holes. Litter covering about the same area was bagged separately. In the laboratory all the samples were placed in ovens at 60°C for about thirty-six hours to dry. The following treatments were then applied to the soil samples from each site: (1) the top 2 cm of soil plus 40 g of litter were heated with the intense flame of a bunsen burner from above for about five minutes (fire does not heat soil substantially below about 1.5 cm in depth; Humphreys and Craig, 1981); (2) half the burnt and half the unburnt samples were covered with 40 g of litter (about 2 cm litter depth); (3) half the samples were given 25 mL water twice weekly; the other half were given 50 mL twice weekly. These quantities corresponded to an even annual precipitation of approximately 115 mm and 230 mm respectively, well below the mean annual rainfall for the sites where the two species occur.

Fifty seeds of *A. distyla* were scattered on the soil surface (beneath any litter) over one half of each container, while fifty seeds of *A. nana* were scattered over the other half. (The containers were partitioned in two by fly-screen gauze dividers). The experimental treatments were arranged in a fully orthogonal design with species and soil provenance.

The numbers of surviving seedlings at the end of four months were analysed by a 5-factor ANOVA with species, fire, litter and water treatments treated as fixed factors, and soil provenance treated as a random factor. Variances were homogeneous (Cochran's statistic = 1.11; $k = 48$, $v = 1$; $P > 0.05$). The above-ground dry weights of harvested seedlings were analysed similarly. Four replicate seedlings were sampled randomly for each treatment combination, except that only two were available in one of the cells. Variances could be stabilized by a square-root transformation of the data with one outlier removed (Cochran's statistic = 0.101; $k = 48$, $v = 3$; $P > 0.05$).

Field experiment

Two replicate sites were chosen within the Sydney region for each of three different ages (times since fire) of vegetation: recently burnt sites (time since fire less than one year) were located in Bouddi NP and Brisbane Water NP north of Sydney; sites burnt nine years previously were in Royal NP and on the Lambert Peninsula in Ku-ring-gai NP and sites burnt twenty-five years previously were located in Royal NP and Bouddi NP. Site localities and floristics are summarised briefly in Table 1.

TABLE 1

Locations and prominent species occurring at sites selected for the field experiment. Grid references are those of the Central Mapping Authority of NSW. Species nomenclature follows Beadle et al. (1982).

Time since fire	Site location 1.	Species occurrence	Site location 2.	Species occurrence
<1 year	Brisbane Water NP GR 414875	<i>Allocasuarina distyla</i> <i>Banksia ericifolia</i> <i>B. oblongifolia</i> <i>Isopogon anemonifolius</i> <i>Darwinia fascicularis</i> <i>Angophora hispida</i> <i>Acacia oxycedrus</i> <i>A. suaveolens</i> <i>Leucopogon microphyllus</i> <i>Epacris microphylla</i>	Bouddi NP GR 473883	<i>Allocasuarina distyla</i> <i>Banksia oblongifolia</i> <i>Hakea dactyloides</i> <i>H. gibbosa</i> <i>Isopogon anemonifolius</i> <i>I. anethifolius</i> <i>Lambertia formosa</i> <i>Angophora hispida</i> <i>Pultenea elliptica</i> <i>Lasiopetalum ferrugineum</i>
9 years	Ku-ring-gai NP GP 408827	<i>Allocasuarina distyla</i> <i>Banksia ericifolia</i> <i>B. oblongifolia</i> <i>Petrophile pulchella</i> <i>Isopogon anemonifolius</i> <i>Hakea teretifolia</i> <i>H. dactyloides</i> <i>H. gibbosa</i> <i>Persoonia lanceolata</i> <i>Acacia oxycedrus</i> <i>A. suaveolens</i> <i>A. ulicifolia</i> <i>Caustis pentandra</i>	Royal NP GR 157205	<i>Allocasuarina distyla</i> <i>Banksia ericifolia</i> <i>B. oblongifolia</i> <i>Persoonia levis</i> <i>Petrophile pulchella</i> <i>Hakea teretifolia</i> <i>Darwinia fascicularis</i> <i>Epacris microphylla</i> <i>Leucopogon microphyllus</i> <i>Dillwynia retorta</i> <i>Olaix stricta</i>
25 years	Bouddi NP GR 470882	<i>Allocasuarina distyla</i> <i>Banksia ericifolia</i> <i>B. oblongifolia</i> <i>Isopogon anethifolius</i> <i>Hakea teretifolia</i> <i>H. gibbosa</i> <i>Woolisia pungens</i> <i>Acacia myrtifolia</i> <i>Lasiopetalum ferrugineum</i>	Royal NP GR 203291	<i>Allocasuarina distyla</i> <i>Banksia ericifolia</i> <i>Banksia marginata</i> <i>Grevillea sericea</i> <i>Isopogon anemonifolius</i> <i>Leucopogon microphylla</i> <i>Acacia ulicifolia</i>

Random co-ordinates were used to locate twenty points within a 15 x 15 m grid at each of the six sites described above. At each point, eighty seeds of *A. distyla* and eighty seeds of *A. nana* were sown over an area of about 15 cm in diameter. The two species were partitioned from one another by fly-screen gauze dividers for ease of seedling identification. The following enclosure treatments were applied to the sown seeds: (1) an ant enclosure; (2) a mammal enclosure; (3) ant and mammal enclosures together; (4) no enclosures; (5) a sham (control) enclosure. Ants were excluded from plots by surrounding them with a cylindrical galvanized iron ring (15 cm diameter, 8 cm deep) which was sunk 3 cm into the ground. The outside of the cylinder was thickly coated in 'tanglefoot', a water-resistant, sticky substance, to deter ants. The control was set up without tanglefoot. Small mammals were excluded from plots by exposure cages made out of PVC mesh (15 x 20 x 10 cm; pore size about 1 cm²). The control was left open on two sides.

In ensuring the efficacy of the enclosure cages it was necessary to interfere with the existing conditions of the treatment plots (such as litter cover) to some extent and care was taken to disturb the uncaged plots comparably. In order to control for the possibility of natural *A. distyla* emergents four additional plots were randomly located at each site and disturbed in a similar manner, except that no seeds were sown. No seedlings emerged at any of these plots over the course of the study. The experimental treatments were orthogonal with species and time since fire, except that the control was arranged asymmetrically in the design (see results). The experiment was commenced in mid April, 1990, and seedlings were finally harvested at the end of August, 1990.

The numbers of emergents after (1) six weeks and (2) four months were analysed by a 5-factor ANOVA with all factors treated as fixed except sites (random and nested in time since fire). Variances in the first analysis were stabilised by $\ln(x + 1)$ transform (Cochran's statistic = 0.076; $k = 60$, $v = 3$; $P > 0.05$); those in the second were established by a $\ln(\ln x + 1) + 1$ data transform (Cochran's statistic = 0.065; $k = 60$, $v = 3$; $P > 0.05$).

There were insufficient numbers of seedlings after four months to allow their dry weights and heights to be analysed in a balanced design of the full experiment. Five seedlings of each species per site were therefore randomly selected from plots at which both ants and mammals had been excluded. (The dry weights and heights of seedlings of *A. distyla* were found not to depend substantially on the enclosure cages). The above-ground dry weights and the heights of these seedlings were analysed by fully balanced 3-factor ANOVAs with species and time since fire treated as fixed factors and site (nested within time since fire) treated as a random factor. A $\ln(x + 1)$ data transform stabilised the variances in both analyses (Cochran's statistic = 0.168, dry weights; = 0.223, heights; $k = 12$, $v = 4$; $P > 0.05$).

RESULTS AND DISCUSSION

The seed rain

The rate at which seed was captured in the seed traps was very low, and there were no easily discernible trends from site to site. For each month from May to August the amount of seed collected was pooled across all sites and ranged from a minimum of 0.25 seeds/week/m² in June to a maximum of 2.3 seeds/week/m² in August. Averaged across all three sites, there were approximately 46 cones/m², or about 3200 seeds/m², in the canopy above the traps. Thus the seed rain per week, expressed in terms of seeds per canopy-stored seed, was very roughly between 8/100 000 (June) and 7/10 000 (August). Over the four months of the study a total of six cones were caught in the traps. This corresponds to a cone-capture rate of 0.11 cones/week/m². Alternatively, 2.4 cones fell per week for every 1000 cones in the canopy.

Of the individual seeds caught in the seed traps, only about 35% were viable. Very few seeds were recovered from the six cones caught in the traps. Those which were released from between the bracteoles were largely decayed and inviable, and only four seeds germinated from the 370 bracteole pairs counted on the cones. This result confirms the finding of Pannell and Myerscough (1993) that cones are abscised from the canopy when they old and after most of the seed has already died.

Spatial and temporal variation in ant harvesting

Seed removal differed significantly between transects within sites ($P < 0.025$), but not between sites ($P > 0.20$). The seeds of the two species were removed at different relative rates between times (species \times time interaction: $P < 0.05$). Marked small-scale spatial variation in rates of seed removal is possibly associated with the territorial foraging patterns of ants and could have important consequences for spatial patterns of seedling recruitment following fire (Andersen, 1988). The lack of significant variation between sites is not surprising; Mossop (1989) found no significant inter-site differences in ant foraging patterns, even between rainforest and dry sclerophyll communities. There were no main effects of time on seed removal rates. Other studies have shown that seed removal rates can be seasonally related to ambient temperature (Cremer, 1965; Christensen, 1971; O'Dowd and Gill, 1984; Andersen and Ashton, 1985; Mossop, 1989) and to stochastic events such as rainfall (Andersen and Ashton, 1985). In the present study, the fact that weather conditions were uniform over the course of observations would account for the relatively low variability in seed harvesting rates over the course of the study.

TABLE 2

ANOVA of numbers of seedlings after 6 weeks and 4 months in the field. There were three random sites within each of the three fixed fire histories (see text). Treatments were fixed: 'Ants' and 'Mammals' are the effects of an ant and mammal exclosure, respectively; 'Cont. vs. ET' is the effect of the sham exclosure control relative to the experimental treatments. $n = 4$ replicates

Source	d.f.	Six weeks		Four months	
		F-ratio	P	F-ratio	P
Fire: F	2	5.95		6.04	
Site: P (F)	3	6.56	<0.001	4.17	<0.01
Species: S	1	75.0	<0.01	101	<0.01
(Treatment): T	(4)				
Cont. vs. ET: C	1	0.706		1.56	
(Among ET): ET	(3)				
Mammals: M	1	5.88		24.2	<0.05
Ants: A	1	11.2	<0.05	11.3	<0.05
AxM	1	0.016		0.20	
FxS	2	4.16		5.23	
FxT	(8)				
FxC	2	0.106		.0145	
FxET	(6)				
FxM	2	0.167		0.235	
FxA	2	1.48		0.684	
FxAxM	2	1.20		6.66	
P (F) xS	3	0.73		0.660	
P (F) xT	(12)				
P (F) xC	3	13.6	<0.001	12.4	<0.001
(F) xET	(9)				
P (F) xM	3	3.99	<0.01	2.54	
P (F) xA	3	3.67	<0.05	3.163	<0.05
P (F) xAxM	3	1.18		0.442	
SxT	(4)				
SxC	1	17.6	<0.05	8.84	
SxET	(3)				
SxM	1	1.58		1.10	
SxA	1	4.17	<0.05	9.95	
SxAxM	1	0.377		0.167	
FxSxT	(8)				
FxSxC	2	6.35		0.964	
FxSxET	(6)				
FxSxM	2	0.202		0.752	
FxSxA	2	0.759		5.19	
FxSxAxM	2	4.95		8.23	
P (F) xSxT	(12)				
P (F) xSxC	3	0.326		0.565	
P (F) xSxET	(9)				
P (F) xSxM	3	0.741		0.823	
P (F) xSxA	3	0.208		0.143	
P (F) xSxAxM	3	0.419		0.265	
Residual	180				
Total	239				

The estimated half-life of a seed under the conditions of the study was 3.56 days, similar to that found by Wellington and Noble (1985) for *Eucalyptus incrassata* seeds and Pierce and Cowling (1991) for seeds of South African fynbos species. It gives an indication

of the order of magnitude which can be expected, but this estimate should be treated with caution since removal rates were almost certainly not constant. The estimated removal rates differed depending on whether all the seeds in the depots were considered (0.177 per day) or whether each depot was treated as a single seed (0.353 per day), with depots spaced by a mean of 3.75m. Other workers have found similar differences (e.g. Andersen, 1988). Hughes and Westoby (1990) suggested that they may reflect the relative proportions of individual and group foragers in the ant community, since group foragers would tend to remove more seeds from fewer depots. This explanation would suggest that, in the present study, group foraging predominated.

It is likely that *A. distyla* and *A. nana* seed removed by ants is consumed in the ants' nests. The alternative possibility that seed removal is a dispersal event is unlikely. The seeds of many legumes are typified by the presence of a specialised food body (elaiosome), a feature which is assumed to be an adaptive reward for seed dispersal agents (Hughes and Westoby, 1990, 1992). However, seeds which provide no food reward for potential dispersal agents (like those of *A. distyla* and *A. nana*) are probably removed to be eaten (Pierce and Cowling, 1991). Ashton (1979) found this to be the case for *Eucalyptus regnans*. Such seed is lost to the potential soil-stored seed bank.

Glasshouse experiment

It has been suggested that the addition of mineral and organic nutrients to the soil resulting from a bush fire may substantially improve the seedling establishment (e.g. Pryor, 1963; Christensen and Muller, 1975; Purdie, 1977; Humphreys and Craig, 1981). This was not the case for *A. distyla* and *A. nana* under glasshouse conditions (F-ratio <1; $P > >0.25$).

In both species more individuals established under the high water treatment relative to the low water treatment ($P < 0.05$), a result which was related to differences in emergence and not to seedling mortality. In the field, levels of soil moisture strongly affect seedling survivorship (e.g. Miles, 1972; O'Dowd and Gill, 1984; Bradstock, 1985). However, this effect is quite different from the moisture effect on emergence found here where ungerminated seeds are dormant and may still germinate under a more favourable moisture regime.

Litter present on the soil may reduce seedling establishment (Williams and Johnson 1992), with seedlings dying before their radicles reach the soil (Purdie, 1977). This appears to have been the case for germinants of *A. nana* rather than for *A. distyla* (compare Figures 1 and 2), a difference which can be explained by the fact that *A. nana* seeds are the smaller and have fewer reserves for initial growth. O'Dowd and Gill (1984) noted the potential increase in seedling mortality with increased litter fall following leaf scorch during fire. They also suggested that post-fire seedling mortality could be partly due to water deficits as a result of increased soil insolation through the burnt canopy. The obvious corollary of this is that litter cover may have a positive effect on seedling recruitment due to the conservation of soil moisture under it (Manders and Richardson, 1992; Keeley, 1992). In the glasshouse litter seemed to have acted in this way on the early recruitment of *A. distyla* seedlings, enhancing recruitment and survivorship of seedlings in each of the soil moisture levels (Figure 1). This suggests that seedling establishment may vary between species with fires of different intensities; increased establishment could be expected for relatively large-seeded plants which can emerge through deep fallen scorched litter following low intensity burns, while the converse could be expected for relatively small-seeded plants which do not have the reserves to emerge from the litter cover.

Field experiment

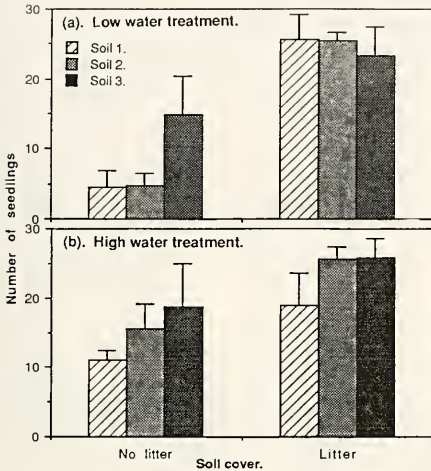
Treatment effects at the end of the four months were already apparent after six weeks (compare analyses in Table 2; see Figures 3 and 4). There was also a reasonably consistent decline in seedling numbers in both species between six weeks and four months

after sowing, a trend more pronounced at sites burnt twenty-five years previously (Figures 3 and 4). Seedling recruitment differed significantly between sites. Although the significant site effect depended on its interaction with the treatment effects (see below), a reasonably consistent trend across all of the treatments was the considerable difference in numbers of recruits between the recently burnt sites and other sites, especially those burnt nine years previously. *A. distyla* responded more to site differences in seedling height and dry weight than *A. nana* (Figure 5; S x P(F) interaction: heights, $P < 0.001$; weights, $P < 0.05$). *A. distyla* seedlings were taller and weighed more at both the recently burnt sites and at sites burnt twenty-five years previously (Figure 5).

A multitude of factors may affect seedling establishment success at the recently burnt sites (Christensen and Muller, 1975; O'Dowd and Gill, 1984; Bradstock, 1991; Williams and Johnson, 1992). Increased insolation was probably important (Miles, 1972), although it is likely that direct competition for biological space at the scale of the seedlings (i.e. close to the ground) was a more important factor at the sites burnt only about a decade ago than at those burnt two and a half decades ago, since the latter had an almost clear understorey. The greater above-ground size of *A. distyla* seedlings grown at the recently burnt sites indicates that they might survive a hot, dry spell in summer better than those which established at unburnt sites. This possibility is foreshadowed by the experimental results. The decline in the number of seedlings between six weeks and four months after sowing was greatest at sites last burnt twenty-five years previously, and it is likely that this difference between sites would have become more pronounced during hot, dry weather in summer (Trabaud and Campant, 1991). Since larger seedlings are more likely to survive conditions in summer, early autumn emergence and subsequent initial establishment during winter can be expected to enhance long-term survivorship. Seedlings which emerge at sites most conducive to fast growth (i.e. burnt sites) are likely to establish best. The corollary of this is that seedlings will establish most successfully at sites burnt in late summer (with *en masse* seed release in early autumn). A similar conclusion was reached by Bradstock (1985) for seedlings of four Proteaceae species.

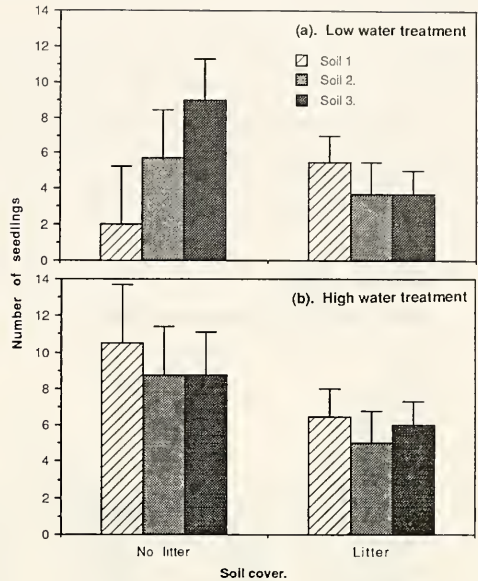
Bradstock (1991) concluded that seedling predation may be important in limiting seedling establishment in proteaceous species at unburnt sites. In the present study, the way in which the enclosure of ants and small mammals influenced seedling establishment was complicated by the significant interactions of the sham enclosure control with species in the first six weeks (Table 2, $P < 0.05$) and its interaction with sites after four months (Table 2, $P < 0.001$). The latter interaction indicates that there was a significant physical effect of the enclosure cages used in the experiment at some sites. For example, there were particularly substantial differences in recruits at recently burnt sites between the null treatment (no enclosures) and sham enclosures (Figure 3a and b). At these sites (to a lesser extent also at sites last burnt nine years previously) the effects of ants and mammals on seedling numbers were confronted by the physical effects of the enclosures. However, in sites last burnt twenty-five years prior to the experiment, the sham enclosures had no significant effect on seedling recruitment (compare Figures 3a and b, and Figures 4a and 4b). In the stands of older vegetation, then, it is reasonable to conclude that the activity of ants and mammals was responsible for reducing the numbers of seedling recruits, especially during the first six weeks (note the significant [$P < 0.05$] P(F) x A and P(F) x M terms in Table 4).

Although the experimental design does not allow statistical discrimination between the individual effects of the two enclosures used, the data suggest that the ant enclosure was chiefly responsible for the confounding effects. This is not surprising as it considerably modified the micro-environment of the experimental plots, most particularly the drainage patterns; seeds surrounded by an ant enclosure would not have been washed away in the heavy rains which fell in the weeks immediately following the experiment's induction, whereas many seeds unprotected in this way were probably lost in the run-off. This would largely account for the fact that the physical effect of the enclosures was promi-



1

Fig. 1. Seedling numbers of *A. distyla* for the glass house experiment. Low water treatment was 25mL twice weekly; high water treatment was 50 mL twice weekly. Soils were taken from different sites (see text for details). Error bars are one SE; n = 4.



2

Fig. 2. Seedling numbers of *A. nana* for the glasshouse experiment. See text for details of experimental treatments. Error bars are one SE; n = 4.

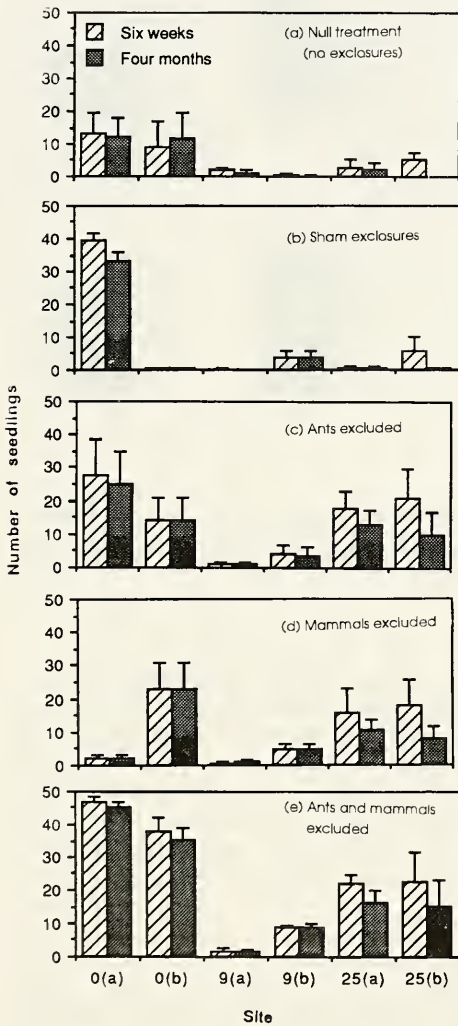
ment at the recently burnt sites where run-off from the bare soil was probably fastest.

The effect of ant activity on seedling numbers was most likely due to their removal of seed, as was foreshadowed by the observation of seed-harvesting by ants reported above. This effect might have been much greater had the period subsequent to seed sowing been warmer and drier (very heavy falls of rain occurred in April). It is now reasonably well established that foraging activity of ants is seasonally related to temperature and that ants are inactive during wet spells (Hughes and Westoby, 1990). This would suggest that seed dispersal may be most effective in cooler months when ant foraging activity is low.

CONCLUSIONS

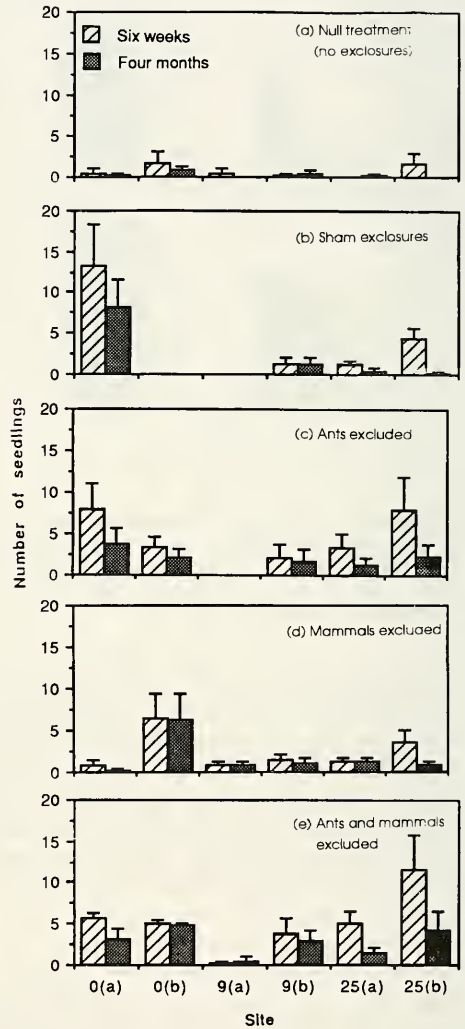
In dense, old (25 years since fire), stands of *A. distyla*, the seed rain ranged between 0.25 and 2.3 seeds/week/m², a figure which probably underestimates the rate typical of summer months. Only about 35% of this seed was viable so that, on average, about one seed capable of germinating fell per square metre each week. Field observations indicate that none of these seeds ever establish as successful seedlings. Some of the possible reasons for this lack of recruitment in the inter-fire period were investigated in this study.

During the period of the study, between 1.3 and 2.4 seeds were removed by ants each week from artificial seed depots separated by a mean distance of about 4 m. It is thus conceivable that a large proportion of the seeds which fall from the canopy in unburnt stands of *Allocasuarina* are harvested and eaten by ants. This hypothesis was supported at some sites by improved seedling establishment within ant exclosures. Viable seeds which escape being eaten by ants (e.g. those which fall prior to a wet period) will germinate under the canopy after sufficient rain. Such germinations are likely to occur occasionally



3

Fig. 3. Seedling numbers of *A. distyla* after 6 weeks and 4 months from 80 seeds sown. See Table 1, for site localities and species lists; see text for details of experimental treatments. 0(a) and 0(b) were sites recently burnt; 9(a) and 9(b) were sites burnt 9 years previously; 25(a) and 25(b) were sites burnt 25 years previously. Error bars are one SE; n = 4.



4

Fig. 4. Seedling numbers of *A. nana* after 6 weeks and 4 months from 80 seeds sown. See Table 1, for site localities and species lists; see text for details of experimental treatments. 0(a) and 0(b) were sites recently burnt; 9(a) and 9(b) were sites burnt 9 years previously; 25(a) and 25(b) were sites burnt 25 years previously. Error bars are one SE; n = 4.

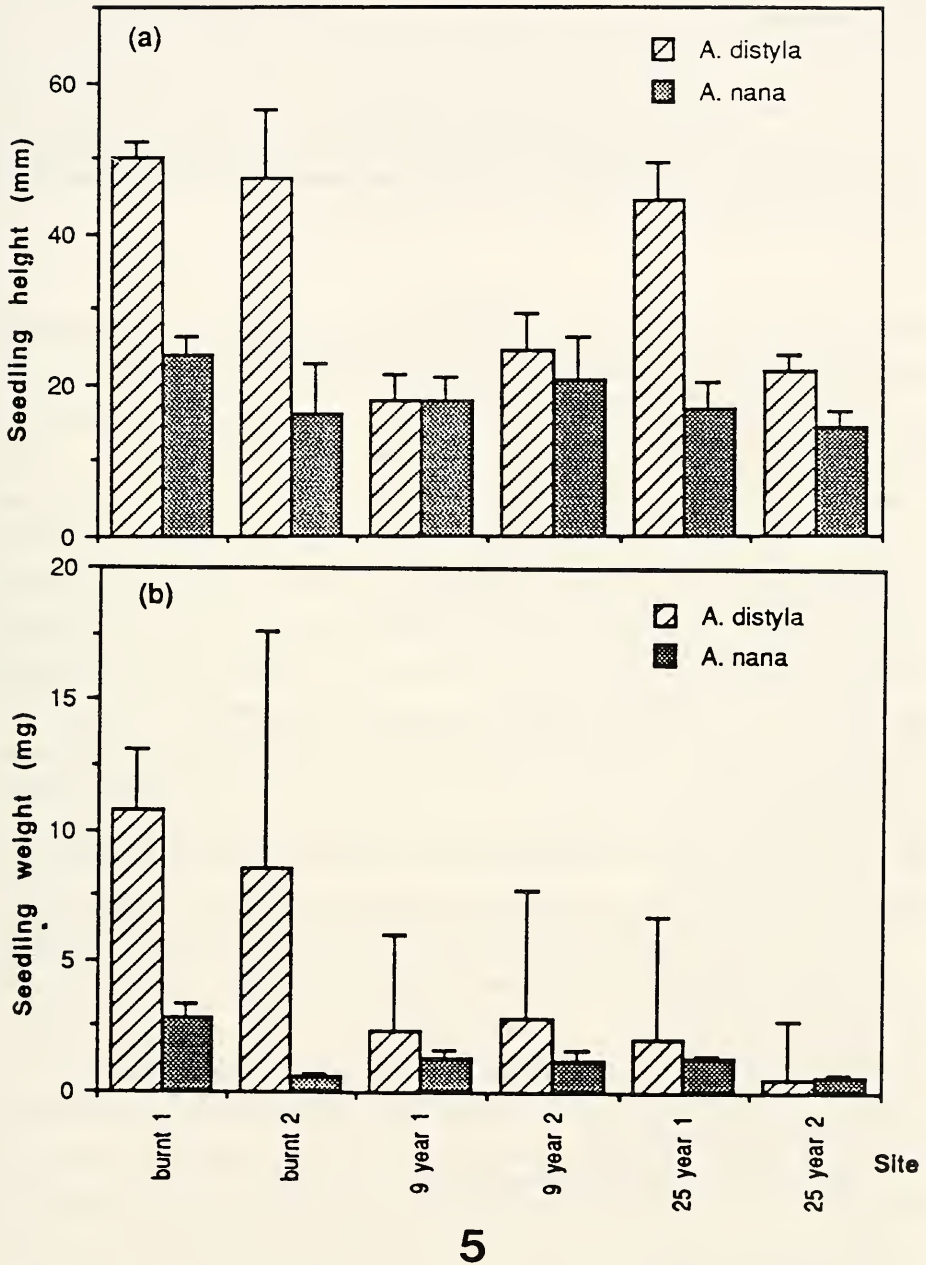


Fig. 5. Above-ground dry weights (a) and heights (b) of *A. distyla* and *A. nana* seedlings harvested after 4 months in the field. See Table 1. for site localities and species lists. Error bars are one SE; n = 5.

in nature, but in contrast to seedlings establishing at recently burnt sites recruitment to adults fails in unburnt stands. The results of this study indicate that whereas a proportion of *Allocasuarina* seedlings may be browsed by small mammals, the chief factors limiting successful establishment under a canopy are likely to be poor light quality and competition for resources.

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